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See also **Bayesianism; Confirmation Theory; Induction, Problem of; Instrumentalism; Realism**

ADAPTATION AND ADAPTATIONISM

In evolutionary biology, a phenotypic trait is said to be an *adaptation* if the trait's existence, or its prevalence in a given population, is the result of natural selection. So for example, the opposable thumb is almost certainly an adaptation: Modern primates possess opposable thumbs because of the selective advantage that such thumbs conferred on their ancestors, which led to the retention and gradual modification of the trait in the lineage leading to modern primates. Usually, biologists will describe a trait not as an adaptation per se but rather as an adaptation *for* a given task, where the task refers to the environmental "problem" that the trait helps the organism to solve. Thus the opposable thumb is an adaptation *for* grasping branches; the ability of cacti to store water is an adaptation *for* living in arid deserts; the brightly adorned tail of the peacock is an adaptation *for* attracting mates; and so on. Each of these statements implies that the trait in question was favored by natural selection *because* it conferred on its bearer the ability to perform the task. In general, if a trait T is an adaptation for task X, this means that T evolved because it enabled its bearers to perform X, which enhanced their Darwinian fitness. This can also be expressed by saying that the *function* of the trait T is to perform X. Thus there is a close link between the concepts of adaptation and evolutionary function (Sterelny and Griffiths 1999; Ariew, Cummins, and Perlman 2002; Buller 1999).

Many authors have emphasized the distinction between a trait that is an adaptation and a trait that is *adaptive*. To describe a trait as adaptive is to say that it is *currently* beneficial to the organisms that possess it, in their current environment. This is a statement solely about the present—it says nothing about evolutionary history. If it turned out that Darwinism were wholly untrue and that God created the universe in seven days, many phenotypic traits would still qualify as adaptive in this sense, for they undeniably benefit their current possessors. By contrast, to describe a trait as an adaptation *is* to say something about evolutionary history, namely that natural selection is responsible for the trait's evolution. If Darwinism turned out to be false, it would follow that the opposable thumb is *not* an adaptation for grasping branches, though it would still be adaptive for primates in their current environment. So the adaptive/adaptation distinction corresponds to the distinction between a trait's *current utility* and its *selective history*.

In general, most traits that are adaptations are also adaptive and vice versa. But the two concepts do not always coincide. The human gastrointestinal appendix is not adaptive for contemporary human beings—which is why it can be removed without loss of physiological function. But the appendix is nonetheless an adaptation, for it evolved to help its bearers break down cellulose in their diet. The fact that the appendix no longer serves this function in contemporary humans does not alter the (presumed) fact that this is why it originally evolved. In general, when a species is subject to rapid environmental change, traits that it evolved in response to previous environmental demands, which thus count as adaptations, may cease to be adaptive in the new environment. Given sufficient time, evolution may eventually lead such traits to disappear, but until this happens these traits are examples of adaptations that are not currently adaptive.

It is also possible for a trait to be adaptive without being an adaptation, though examples falling into this category tend to be controversial. Some linguists and biologists believe that the capacity of humans to use language was not directly selected for, but emerged as a side effect of natural selection for larger brains. According to this theory, there was a direct selective advantage to having a large brain, and the emergence of language was simply an incidental by-product of the resulting increase in brain size among proto-humans. *If* this theory is correct, then human linguistic ability does not qualify as an adaptation and has no evolutionary function; thus it would be a mistake to look for a specific environmental demand to which it is an evolved response. But the ability to use language is presumably adaptive for humans in their *current* environment, so this would be an example of an adaptive trait that is not an adaptation. It should be noted, however, that many biologists and linguists are highly suspicious of the idea that human linguistic capacity was not directly shaped by natural selection. (See Pinker and Bloom 1990 and Fodor 2000 for opposing views on this issue.)

It sometimes happens that a trait evolves to perform one function and is later co-opted by evolution for a quite different task. For example, it is thought that birds originally evolved feathers as a way of staying warm, and only later used them to assist with flight. This is an interesting evolutionary phenomenon, but it creates a potential ambiguity. Should birds' feathers be regarded as an adaptation for thermoregulation or for efficient flight? Or perhaps for both? There is no simple answer to this question, particularly since feathers underwent considerable evolutionary modification after they first began to be used as a flying aid. Gould and Vrba (1982) coined the term "exaptation" to help resolve this ambiguity. An exaptation is any trait that originally evolves for one use (or arises for nonadaptive reasons) and is later co-opted by evolution for a different use.

How is it possible to tell which traits are adaptations and which are not? And if a particular trait is thought to be an adaptation, how is it possible to discover what the trait is an adaptation *for*, that is, its evolutionary function? These are pressing questions because evolutionary history is obviously not directly observable, so can be known only via inference. Broadly speaking, there are two main types of evidence for a trait's being an adaptation, both of which were identified by Darwin (1859) in *On the Origin of Species*. First, if a trait contributes in an obvious way to the "fit" between organism and environment, this is a prima facie reason for thinking it has been fashioned by natural selection. The organism/environment fit refers to the fact that organisms often possess a suite of traits that seem specifically tailored for life in the environments they inhabit. Consider for example the astonishing resemblance between stick insects and the foliage they inhabit. It seems most unlikely that this resemblance is a coincidence or the result of purely chance processes (Dawkins 1986, 1996). Much more plausibly, the resemblance is the result of many rounds of natural selection, continually favoring those insects who most closely resembled their host plants, thus gradually bringing about the insect/plant match. It is obvious *why* insects would have benefited from resembling their host plants—they would have been less visible to predators—so it seems safe to conclude that the resemblance is an adaptation for reducing visibility to predators. Biologists repeatedly employ this type of reasoning to infer a trait's evolutionary function.

Second, if a phenotypic trait is highly *complex*, then many biologists believe it is safe to infer that it is an adaptation, even if the trait's evolutionary function is not initially known. Bodily organs such as eyes, kidneys, hearts, and livers are examples of complex traits: Each involves a large number of component parts working together in a coordinated way, resulting in a mechanism as intricate as the most sophisticated man-made device. The inference from complexity to adaptation rests on the assumption that natural selection is the only serious scientific explanation for how organic complexity can evolve. (Appealing to an intelligent deity, though intellectually respectable in pre-Darwinian days, no longer counts as a serious explanation.) Again, inferences of this sort do not strictly amount to proof, but in practice biologists routinely assume that complex organismic traits are adaptations and thus have evolutionary functions waiting to be discovered.

The definition of an adaptation given above—any trait that has evolved by natural selection—is standard in contemporary discussions. In this sense, all biologists would agree that every extant organism possesses countless adaptations. However, the term has sometimes been understood slightly differently. R. A. Fisher, one of the founders of modern Darwinism, wrote that an organism

> "is regarded as adapted to a particular situation . . . only in so far as we can imagine an assemblage of slightly different situations, or environments, to which the animal would on the whole be less well adapted; and equally only in so far as we can imagine an assemblage of slightly different organic forms, which would be less well adapted to that environment." (1930, 41)

It is easy to see that Fisher's notion of adaptation is more demanding than the notion employed above. Fisher requires a very high degree of fit between organism and environment before the concept of adaptation applies, such that any small modification of either the organism or the environment would lead to a reduction in fitness. In modern parlance, this would normally be expressed by saying that the organism is *optimally* adapted to its environment.

It is quite possible for an organism to possess many adaptations in the above sense, i.e., traits that are the result of natural selection, without being optimally adapted in the way Fisher describes. There are a number of reasons why this is so. First, natural selection is a gradual process: Many generations are required in order to produce a close adaptive fit between organism and environment. Suboptimality may result simply because selection has yet to run its full course. Second, unless there is considerable environmental constancy over time, it is unlikely that organisms will evolve traits that adapt them optimally to any particular environment, given the number of generations required. So suboptimality may result from insufficient environmental constancy. Third, there may be evolutionary trade-offs. For example, the long necks of giraffes enable them to graze on high foliage, but the price of a long neck might be too high a center of gravity and thus a suboptimal degree of stability. Evolution cannot always modify an organism's phenotypic traits independently of each other: Adjusting one trait to its optimal state may inevitably bring suboptimality elsewhere. Finally, as Lewontin (1985) and others have stressed, natural selection can drive a species from one point in phenotypic space to another only if *each intermediate stage* is fitness enhancing. So, suboptimality may result because the optimal phenotypic state cannot be accessed from the actual state by a series of incremental changes, each of which increases fitness. For all these reasons, it is an open question whether natural selection will produce optimally adapted organisms.

It is worth noting that the Fisherian concept of optimal adaptation employed above is not *totally* precise, and probably could not be made so, for it hinges on the idea of a small or slight modification to either the organism or the environment, leading to a reduction in fitness. But "small" and "slight" are vague terms. How large can a modification be before it counts as too big to be relevant to assessing whether a given organism is optimally adapted? Questions such as this do not have principled answers. However, any workable concept of optimality is likely to face a similar problem. It is unacceptable to say that an organism is optimally adapted if there is no *possible* modification that would raise its fitness, for by that token no organism would qualify as optimally adapted. With sufficient imagination, it is always possible to think of phenotypic changes that would boost an organism's fitness—for example, doubling its fecundity while leaving everything else unchanged. (As John Maynard Smith wrote, "it is clearly impossible to say what is the "best" phenotype unless one knows the range of possibilities" [Maynard Smith 1978, 32]). So to avoid trivializing the concept of optimality altogether, some restriction must be placed on the class of possible modifications whose effects on organismic fitness are relevant to judging how well adapted the organism is in its current state. Spelling out the necessary restriction will lead to a concept similar to Fisher's, with its attendant vagueness.

The constraints on optimality noted in the earlier discussion of suboptimality show that natural selection *may* fail to produce organisms that are optimally adapted. But how important these constraints are in practice is a matter of considerable controversy. Some biologists think it is reasonable to assume that most extant organisms are optimally or nearly optimally adapted to their current environment. On this view, any phenotypic trait of an organism can be studied on the assumption that selection has fine-tuned the trait very precisely, so that there is an evolutionary reason for the character being exactly the way it is. Other biologists have less confidence in the power of natural selection. While not denying that selection *has* shaped extant phenotypes, they see the constraints on optimality as sufficiently important to invalidate the assumption that what has actually evolved is optimal in Fisher's sense. They would not seek adaptive significance in every last detail of an organism's phenotype. (See Maynard Smith 1978 and Maynard Smith et al. 1985 for a good discussion of this issue.)

The optimality question is just one aspect of an important and sometimes heated debate concerning the legitimacy of what is called "adaptationism" in evolutionary biology (Sober and Orzack 2001; Dupre 1987). Adaptationism encompasses both an empirical thesis about the world and a methodology for doing evolutionary research (Godfrey-Smith 2001). Empirically, the main claim is that natural selection has been by far the most important determinant of organismic phenotypes in evolutionary history—all or most traits have been directly fashioned by natural selection. Typically, adaptationists will also show some sympathy for the view that extant organisms are optimally adapted to their environments, in at least certain respects. Methodologically, adaptationists believe that the best way to study the living world is to search for the evolutionary function of organisms' phenotypic traits. Thus, for example, if an adaptationist observes an unusual pattern of behavior in a species of insect, the adaptationist will immediately assume that the behavior has an evolutionary function and will devote effort to trying to discover that function. Opponents of adaptationism reject both the empirical thesis and the methodological strategy. They emphasize the constraints on optimality noted above, as well as others; additionally, they point out that natural selection is not the only cause of evolutionary change and that organisms possess certain features that are nonadaptive and even maladaptive. Thus, it is a mistake to view the living world through an exclusively adaptationist lens, they argue.

The basic contours of the adaptationism debate have been in place for a long time, and indeed trace right back to Darwin. But the modern debate was instigated by Stephen Jay Gould and Richard Lewontin's famous article "The Spandrels of San Marco and the Panglossian Paradigm" (Gould and Lewontin 1979). These authors launched a forthright attack on what they saw as the extreme adaptationism prevalent in many evolutionary circles. They accused adaptationists of (a) uncritically assuming that every organismic trait *must* have an evolutionary function, (b) failing to accord a proper role to forces other than natural selection in evolution, and (c) paying insufficient heed to the constraining factors that limit selection's power to modify phenotypes at will. Unusually for a scientific article, "Spandrels" contains two striking literary allusions. Firstly, adaptationists are compared to Dr. Pangloss, a protagonist in Voltaire's satirical novel *Candide*, who despite suffering terrible misfortunes continues to believe that he inhabits the "best of all possible worlds." Gould and Lewontin's suggestion is that adaptationists commit a similar absurdity by viewing every aspect of an organism's phenotype as optimized by selection. Secondly, adaptationists are accused of inventing "Just So Stories" in their relentless search for evolutionary functions, that is, devising speculative hypotheses about traits' adaptive significance that owe more to their ingenuity than to empirical evidence. The reference here is to Rudyard Kipling's famous collection of children's stories, which include "How the Leopard Got Its Spots" and "How the Camel Got His Hump."

The title of Gould and Lewontin's paper illustrates what is perhaps their central complaint against adaptationist logic: the assumption, in advance of specific empirical evidence, that every trait has adaptive significance of its own. *Spandrel* is an architectural term that refers to the roughly triangular space between two adjacent arches and the horizontal above them; they are necessary by-products of placing a dome (or a flat roof) on arches. The spandrels beneath the great dome of St. Mark's Cathedral in Venice are decorated with elaborate mosaics of the four evangelists. Gould and Lewontin's point is that despite their ornate design, the spandrels are obviously not the raison d'être of the whole construction: Rather, they are inevitable by-products of the architectural design. Similarly, they suggest, certain anatomical and morphological traits of modern organisms may be inevitable by-products of their overall design, rather than directly shaped by selection. If so, such traits would not be adaptations, and it would be inappropriate to search for their evolutionary function. The human chin is a commonly cited example of a spandrel.

Gould and Lewontin's attack on adaptationism provoked an array of different reactions. Some of their opponents accused them of caricaturing adaptationism and thus attacking a strawman, on the grounds that no evolutionist had ever claimed every phenotypic trait of every organism to be adaptation, less still an optimal adaptation. There is certainly an element of truth to this charge. Nonetheless, Gould and Lewontin were writing at the height of the controversy over human sociobiology; and it is also true that *some* of the early proponents of that discipline advanced highly speculative hypotheses about the supposed evolutionary function of various behavioral patterns in humans, often on the basis of flimsy and anecdotal evidence. (This was not true of the best work in human sociobiology.) Gould and Lewontin's critique, even if overstated, was a useful corrective to this sort of naive adaptationism and led to a greater degree of methodological self-awareness among evolutionary biologists.

With hindsight, it seems that Gould and Lewontin's article has tempered, but not altogether eliminated, the enthusiasm felt by evolutionary biologists for adaptationism (cf. Walsh, "Spandrels," forthcoming). Many biologists continue to believe that cumulative natural selection over a large number of generations is the most plausible way of explaining complex adaptive traits, and such traits are abundant in nature. And despite the potential methodological pitfalls that the "Spandrels" paper warns against, the adaptationist research program continues to be highly fruitful, yielding rich insights into how nature works, and it has no serious rivals. Moreover, it *is* possible to test hypotheses about the adaptive significance of particular traits, in a variety of different ways. The *comparative method,* which involves comparing closely related species and trying to correlate phenotypic differences among them with ecological differences among their habitats, is one of the most common (cf. Harvey and Pagel 1991); it was employed by Darwin himself in his discussion of the Galapagos finches' beaks. Experimentally altering a trait, e.g., painting the plumage of a bird, and then carefully observing the effect on the organism's survival and reproductive success is another way of learning about a trait's adaptive significance. The most sophisticated work in evolutionary biology routinely uses these and other tests to adjudicate hypotheses about evolutionary function, and they bear little relation to the crude storytelling that Gould and Lewontin criticize. (See Endler 1986 for a good discussion of these tests.)

On the other hand, there is a grain of truth to Gould and Lewontin's charge that when a particular hypothesis about a trait's adaptive function is falsified, biologists will normally invent another adaptationist hypothesis rather than conclude that the trait is not an adaptation at all. However, not everyone agrees that reasoning in this way is methodologically suspect. Daniel Dennett agrees that adaptationists like himself offer "purely theory-driven explanations, argued a priori from the assumption that natural selection tells the true story—some true story or other—about every curious feature of the biosphere," but he regards this as perfectly reasonable, given the overall success of Darwinian theory (1995, 245). It is doubtful whether what Dennett says is literally true, however. There are many "curious features" of the biosphere for which it is not known whether there is an adaptationist story to be told or not. Take for example the prevalence of repeat sequences of noncoding "junk" DNA in the eukaryotic genome. This certainly qualifies as a curious feature—it took molecular biologists greatly by surprise when it was first discovered in the 1970s. But junk DNA has no known function—hence its name—and many people suspect that it has no function at all (though the current evidence on this point is equivocal; see Bejerano et al. 2004 for a recent assessment). So although Dennett is right that there is a general presumption in favor of adaptationist explanations among biologists, it is not true that every trait is *automatically* assumed to be an adaptation.

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See also **Evolution; Fitness; Natural Selection**